

**NEW SYNONYMY IN CROTON SECT. GEISELERIA
(EUPHORBIACEAE) FROM THE CARIBBEAN AND A NEW
SUBSPECIES OF CROTON GUILDINGII FROM VENEZUELA**

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ABSTRACT. Analysis of the *Croton guildingii* species complex in sect. *Geiseleria* leads to the synonymy of several formerly obscure species names of *Croton* in Venezuela and adjacent islands of the Lesser Antilles. *Croton guildingii* subsp. *tiarensis* from the Interior Coastal Range of northern Venezuela is newly described and illustrated. This subspecies occurs in a small region of serpentine outcrops and is one of the first examples of adaptation to serpentine soils in the genus outside of Cuba.

Croton L. is the second largest genus in the Euphorbiaceae, with 1,223 species recognized at the time by Govaerts et al. (2000). Webster (1993) divided the genus into 40 sections, and the first molecular study of the genus by Berry et al. (2005) provided support for some of those sections, but showed others to be polyphyletic. Since then, molecular sampling in the genus has increased substantially, and studies of particular groups are emerging or should soon be published (Riina 2006; Van Ee 2006; Van Ee et al., in press).

One group currently under revision by the second author is sect. *Geiseleria* (Kl.) Baill. It was characterized by Webster (1993) as consisting of monoecious herbs or small shrubs with stellate indumentum; alternate, dentate leaves with petiolar glands; entire stipules; terminal inflorescences with lower pistillate flowers and upper staminate ones; reduced petals in the pistillate flowers; entire, unequal sepals; and bifid styles. Additional characters we have found to be diagnostic of most species in the section include persistent linear-curved bracteoles on the male flowers even after the flowers have dehisced; the presence of stalked glands in some or all of the sinuses of the leaf margin; and a generally persistent pistillate calyx that emerges from a distinctive, smooth, cup-shaped receptacle that is most readily observed once the fruit has dehisced (see Fig. 1C).

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Our study began with the ecological analysis by the junior author of the vegetation on a small serpentine soil outcrop in the Interior Coastal Range of northern Venezuela (Barreto & Casale 2002). A series of collections was made of a *Croton* that was not matched to any species present in the National Herbarium (VEN). We initially intended to describe these gatherings as a new species, but upon closer examination of other specimens on loan for the revision of sect. *Geiseleria*, we discovered that they formed part of a species complex ranging across the northern coast of South America and into the Lesser Antilles.

- Croton guildingii*** Griseb., Fl. Brit. West Indies 38. 1859.—TYPE: ST. VINCENT AND THE GRENADINES. St. Vincent, 1822, *Rev. L. Guilding s.n.* (holotype: K!).
Croton wulfschlaegelianus Muell. Arg., Flora 55: 10. 1872.—TYPE: GRENADA. 1847, H. R. Wulfschlägel 1004 (holotype: M!).
Croton guaricensis Croizat, Mem. Soc. Cien. Nat. La Salle (Caracas) 10(26): 125. 1950.—TYPE: VENEZUELA. Guárico: Distrito Infante, inmediaciones del Río Perro a unos 20 km al norte de Espino, en selva veranera en las márgenes de la carretera, 2 Apr 1950, *L. Croizat s.n.*, (holotype: CAR #830!; isotype: F!).
Croton novaespartae Croizat, Mem. Soc. Cien. Nat. La Salle (Caracas) 10(26): 124. 1950.—TYPE: VENEZUELA. Nueva Esparta: Isla Margarita, planicie entre San Juan y La Asunción, común en lugares áridos, Sep 1948, *L. Croizat s.n.* (holotype: CAR #838!; isotype: F!).
Croton larensis Steyerl., Fieldiana, Bot. 28(2): 314. 1952.—TYPE: VENEZUELA. Lara: dry chaparral between Trujillo-Lara boundary and Carora, 305 m, 28 May 1944, *J. A. Steyermark 58606* (holotype: F!).

As recognized here, *Croton guildingii* is a widespread species known from the Windward Islands of the Lesser Antilles (Grenada, Martinique, St. Lucia, and St. Vincent), the Venezuelan island of Margarita, the northern coastal region of Venezuela from Estado Sucre in the east to Estado Zulia in the west, and probably into northeastern Colombia as well. A closely related, but larger and more robust species appears to be *C. jutiapensis* Croizat, from Guatemala, Honduras, Nicaragua, and Costa Rica. All of the names listed here in synonymy clearly apply to *C. guildingii*, except that the type of *C. guaricensis* has very few diagnostic floral characters available. Nonetheless, it is unambiguously a member of sect. *Geiseleria*, with the stipitate leaf sinus glands, one or two pairs of stalked petiolar glands, and the persistent, curved male bracteoles with distinctive glands at the base. It furthermore has the typical ochraceous pubescence of *C. guildingii* and appears to have regular dichotomous branching.

Diagnostic characters of *C. guildingii* include the golden young pubescence, the relatively low number of secondary veins (3–7 per side of the midvein), the small bottle-shaped glands at the base of the bracts, the unequal sepals, vestigial pistillate petals, the fairly regular presence of stalked marginal glands in at least some of the leaf sinuses, the presence of 1 to 3 pairs of stalked petiolar glands, and the conspicuous floral receptacle after fruit dehiscence. Distinctive populations of *C. guildingii* that we deem worthy of separate taxonomic status are described below as a new subspecies.

- Croton guildingii*** subsp. ***tiarensis*** P. E. Berry & R. Riina, subsp. nov.—TYPE: VENEZUELA. Aragua: Loma de Hierro, Km 15 antes de la mina de níquel, laderas con sabana de *Trachypogon* con arbustos bajos dispersos y algunos parches de

Agave, 10°80'50"N, 63°55'W, 1200 m, 1 Aug 2001, R. Riina, P. E. Berry & C. Reyes 1274 (holotype: MICH!; isotypes: F! GH! NY! US! VEN! WIS!).

Croton lagunillae Croizat, Mem. Soc. Cien. Nat. La Salle (Caracas) 10(26): 122. 1950.—TYPE: VENEZUELA. Mérida: Región xerófila en las inmediaciones de Lagunillas, 1949, G. Marcuzzi s.n. (holotype: CAR # 837!; isotype: F!).

Croton marcuzzianus Croizat, Mem. Soc. Cien. Nat. La Salle (Caracas) 10(26): 123. 1950.—TYPE: VENEZUELA. Mérida: Región xerófila en las inmediaciones de Lagunillas, 1949, G. Marcuzzi s.n. (holotype: CAR #836!; isotype: F!).

Fig. 1.

Frutex 0.5–2.5 m altus sectio *Geiseleria* pertinens, ab *Croton guildingii* tipico foliis dense aureo-pubescentibus rigidis, inflorescentia 1.5–3.5 cm longa, habito fortiter dichotomo, in terra ophiolithica crescenti differt.

Loosely and strongly dichotomously branched shrub 0.5–2.5 m tall, monocious; young stems densely golden-stellate, older stems reddish to greyish, glabrate, and lenticellate, to 8 mm in diameter; no latex noted when stems were freshly cut. Leaves elliptic-ovate, firmly membranous and rigid, 3–5 × 1.1–3 cm, apex acute to subrounded, base rounded to cuneate, margin coarsely dentate, often with subsessile to stipitate glands present in the sinuses, venation parallel with 3–6 secondary veins on either side of the midvein, upper surface pale to golden-green with a dense covering of porrect-stellate trichomes, but the leaf surface still visible underneath, lower surface paler and with a denser, whiter covering of stellate trichomes, the ones on the main veins larger than the trichomes on the surface in between; petiole 5–10 mm long, densely stellate-pubescent, with 1 (–3) pairs of subsessile to shortly stipitate, saucer-shaped glands 0.7–1 mm in diameter positioned laterally between the two surfaces of the adjacent leaf blade, the surface yellow-lustrous when fresh; stipules filiform, stellate-pubescent, caducous, 2–3 mm long. Inflorescences terminal, erect, sometimes a fruit remaining in the axil of two younger dichotomous flowering branches, 1.5–3.5 (–4) cm long, 1–5 pistillate flowers towards the base, numerous staminate flowers towards the tip, rachis densely golden stellate-pubescent. Staminate flowers with a thin, persistent pedicel 1.5–2 mm long with scattered porrect-stellate trichomes and persistent bottle-shaped glands at the base; sepals 5, valvate, elliptic, acute, 2–3 × 1.5–2.5 mm, villous on the inner surface, stellate-pubescent on the outer surface, whitish; petals 5, elliptic, ovate, 2–3 × 1.5–2.5 mm, villous on both surfaces, white; stamens 10–11, filaments inflexed in bud, 2–3 mm long at anthesis, the receptacle villous; anthers 0.8 × 0.3–0.4 mm. Pistillate flowers with pedicel 0.5–2.5 mm long, subtended by a densely pubescent filiform bract 3–6 mm long; sepals 5, oblong to narrowly obovate, 3–5 × 1.5–2.5 mm, apex rounded, densely stellate-pubescent on the outer surface, well separated from each other at anthesis, slightly unequal in size; petals 2–3 mm long, filiform, pubescent; ovary spheroid, ca. 5 mm in diameter, densely covered by golden-stellate trichomes 1–1.5 mm long; styles bifid, basally pubescent, suberect, 3–5 mm long. Capsules ca. 6 mm in diameter, with a conspicuous receptacle ca. 2 mm in diameter visible after dehiscence, the perianth and columella persistent. Seeds broadly oblong, 4 mm long, 3 mm wide, 2.5 mm thick, surface smooth to slightly longitudinally striate, light tan, carunculate, the caruncle yellowish white, 2.5 mm wide, 1 mm high, thicker in the middle.

Distribution (Fig. 2). Mainly restricted to the Serranía del Interior of the Venezuelan Cordillera de la Costa, along south-facing slopes of Loma de Hierro north of Tiara in Estado Aragua and in adjacent parts of Estado Miranda, Venezuela, from 1000 to 1250 m elevation. Also present near Lagunillas, Estado Mérida, in a semi-arid interandean valley at 800 to 900 m elevation.

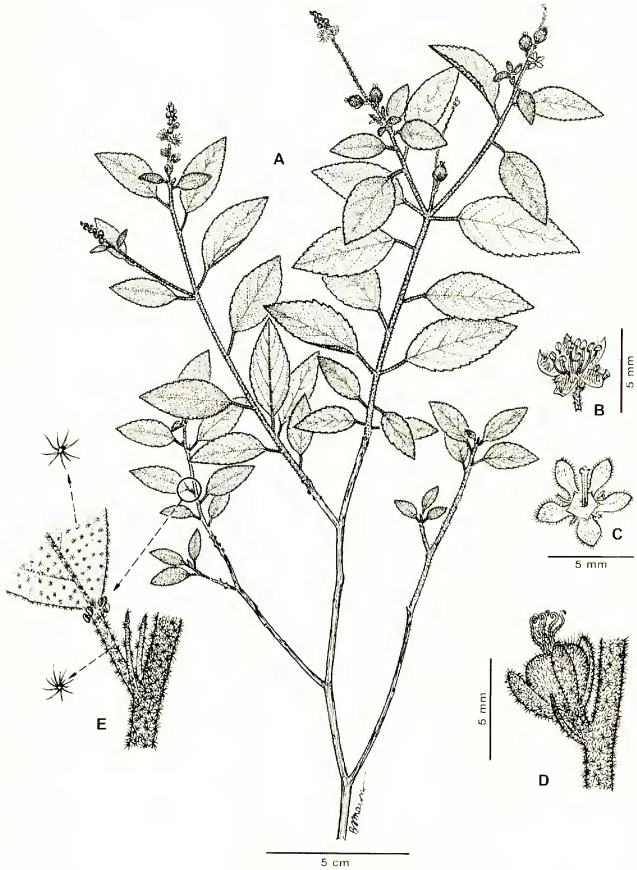


FIG. 1. *Croton guildingii* subsp. *tiarensis*. A. Habit. B. Male flower at anthesis. C. Pistillate perianth remaining after fruit dehiscence; note the spatulate sepals, the filiform petals and the persistent columella. D. Pistillate flower at anthesis, with filiform bract. E. Detail of a leaf base, petiolar glands, stipules, and stellate trichomes. (Based on Riina et al. 1274.)

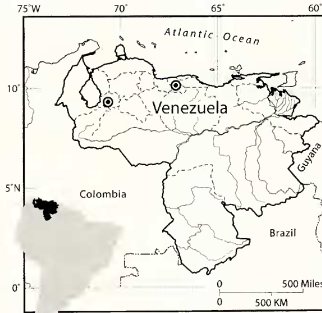


FIG. 2. Distribution of *Croton guildingii* subsp. *tiarensis* in Venezuela.

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** ARAGUA: Certos arriba de Tiara, 24 Jul 1952, *Schnee 1072* (F).—ARAGUA-MIRANDA: Loma de Hierro, en sabana de *Trachypogon*, 24 Mar 2000, *Barreto & Casale 84* (MICH, VEN), *Barreto & Casale 100* (MICH, VEN), *Barreto 109* (MICH), 10 May 2000, *Barreto 159* (MICH), 5 Oct 2000, *Barreto & Casale 138* (MICH, VEN), *Barreto & Casale 169* (MICH, VEN).

An unusual feature of this new subspecies is that it is one of the first taxa of *Croton* in South America that is largely restricted to serpentine outcrops, which are rare there. Serpentine outcrops are well known for their high levels of plant endemism, due in part to the toxicity of heavy metals, such as nickel, chromium, cobalt, and manganese (Kruckeberg 1986). On the Caribbean island of Cuba, there are large areas of serpentine outcrops scattered across the country, and these areas account for much of the species-level and genus-level endemism in Cuba (Borhidi 1985, 1996). Several species of *Croton* sect. *Cascarilla* Griseb. are restricted to serpentine outcrops on Cuba, as well as five of the six species of sect. *Moacroton* (Van Ec et al., in press). Outside of Cuba and Hispaniola, we have found no reliable records of *Croton* species known to be restricted to serpentine barrens and, indeed, no records to date of any member of sect. *Geiseleria* growing in serpentine areas.

Croton guildingii subsp. *tiarensis* is the dominant shrub where it occurs locally on rocky, serpentine outcrops covered mainly by *Trachypogon* grasses and occasional *Agave* plants. The shrubs are scattered in a predominantly herbaceous vegetation cover and occur both on open slopes and in more protected gulleys. Depending on the exposure and the microsite, mature plants vary from 0.5 to 2.5 m high. Towards the larger end of this scale, the shrubs are loosely and dichotomously branched. This area is one of the main nickel-producing regions in Venezuela, and, indeed, there is a large mining operation centered downslope towards the town of Tiara and operated by the company Cerro de Níquel. *Croton guildingii* subsp. *tiarensis* appears to be locally restricted to this serpentine outcrop, which forms a narrow east-west band 60 km long in easternmost Aragua State and westernmost Miranda State (Beck 1986). This outcrop is known as the Tiara Formation and is of volcanic origin during the middle Cretaceous (Smith 1952). Barreto and Casale (2002) used the semiquantitative

dimethylglyoxime method to test for the presence of nickel in the plant tissue of species occurring in this serpentine area of northern Venezuela, and *C. guildingii* subsp. *tiarensis* tested positive for nickel accumulation.

Nuclear ITS and plastid *trnL-trnF* intron and spacer DNA sequence data from Riina et al. 1274 (Berry et al. 2005) places *C. guildingii* subsp. *tiarensis* squarely within section *Geiseleria* and most closely allied to *C. glandulosus* L. and *C. martinianus* V. M. Steinm. The former is a widespread, weedy, and semiherbaceous species, and the latter is a Mexican endemic, but neither is known to be associated with serpentine substrates. Subspecies *tiarensis* differs from the nominate subspecies of *C. guildingii* in its stiffer, generally smaller, and more densely pubescent leaves, the nearly equal sepals, its strongly dichotomous branching pattern, shorter inflorescences, and its propensity for inhabiting unusual substrates, such as serpentine barrens and sodium bicarbonate deposits.

Both of the names here listed in synonymy have been virtually ignored until now, because they apply to taxa known only from their rather meager type specimens, collected at the same locality by the same collector, for which the sectional placement was not ascertained by Croizat (1950). Examination of the types shows that they both possess characters diagnostic of *C. guildingii*, but they approach subsp. *tiarensis* more in their rigid, densely pubescent leaves, dense golden pubescence on young growth, and sepals that are nearly equal in size. The area where they were collected in the Andes near Lagunillas, Estado Mérida, is characterized as an unusual "semi-arid enclave" caused by a rain shadow between the tall mountain ranges on either side of the Río Chama valley (Naranjo et al. 2003); the lagoons after which Lagunillas was named are major deposits of sodium calcium carbonate, which may also restrict the kinds of plants that can occur there in the surrounding town scrub vegetation.

The epithet of the new subspecies refers to the town of Tiara, Estado Aragua, which is the village closest to the type locality. It also acknowledges our co-collector Carlos Reyes, since his surname as well as the name of the town both have connotations of royalty.

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